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THE human brain is the most complicated organ known, and although its anatomy has been the object of innumerable investigations, often by observers of the highest ability, we are still far from understanding its organization. Within recent years, however, embryologists have turned to the study of the development of the brain, and have succeeded in elucidating many of the obscure features. Here, as in so many other cases, embryology has furnished the master-key to unlock the mystery of the adult anatomy. The series of conceptions which we have derived from our present knowledge of the development of the brain are so clearly established that I regard them as impregnable. They are so far in advance of all previous achievements in the study of the brain that they may be called almost revolutionary, and they are of so fundamental a character that the entire anatomy of the brain and the entire physiology of the brain must be recast to agree with our embryological results.

The present article is an attempt to summarize, as simply as possible, the principal conclusions of recent researches on the nervous system.

Physiologists have long been accustomed to divide nerve fibers into two classes: efferent, or those which carry out impulses; and afferent, or those which carry in nerve impulses to the nervous system. Not infrequently the less accurate terms sensory and motor are used as synonymous with afferent and efferent respectively. The nerves are bundles of nerve fibers, and each nerve is supposed to have typically two roots—one sensory, by which all the sensory fibers enter, and the other motor, by which all the efferent fibers leave, the nervous system. It was supposed that

every nerve fiber was connected with a nerve cell in the central nervous system, and that the nerve fibers grew out from the central nervous system. It has long been known that various nerves have thickenings at certain points; the thickenings are the so-called ganglia and they contain nerve cells. The cells in these ganglia were supposed to have migrated from the central parts along the nerves.

The preceding recapitulation of familiar elementary facts will serve to emphasize the following new conclusions: 1. The nervous system consists of two parts, which differ so markedly in their origin and differentiation that it would be hardly an exaggeration to say that there are two nervous systems, for the original duality is never obliterated. The two parts I shall term the *medullary* and the *ganglionic* respectively. Each part has its special typical cells and nerve fibers. It is further probable that there is still a third class of nerve fibers—namely, those connected with the sensory apparatus of the special sense cells. 2. There are *three* sets of nerve roots—namely, the true *dorsal* roots, which are formed solely by ganglionic nerve fibers; and the *lateral* and the *ventral* roots, which are formed solely of medullary nerve fibers; the lateral roots have been hitherto generally confused with the dorsal roots; they have been traced heretofore only in the brain and in the cervical nerves, but I consider it more than possible that the posterior roots of the spinal nerves will be found to represent both dorsal and lateral roots. 3. Nerve fibers grow out from a cell and the end of each fiber branches; but, so far as observed, none of the branches become materially continuous, either with other nerves or nerve cells or with any other cells or other protoplasmatic structures. 4. The entire brain and spinal cord is divided into four principal longitudinal divisions, which I have named after their discoverer the *zones of His.* The zones are in pairs—that is to say, on each side there is a *dorsal* (i. e., in the spinal cord "posterior") and a *ventral* (i. e., in the spinal cord "anterior") zone. These zones are of fundamental importance, because all the fibers which belong to the ganglionic portion of the nervous system ramify in the dorsal zone, while all the fibers belonging to the medullary portion leave the spinal cord (or brain) through the ventral zone. Both zones persist throughout life, and preserve their fundamental relations to the two kinds of nerve fibers.

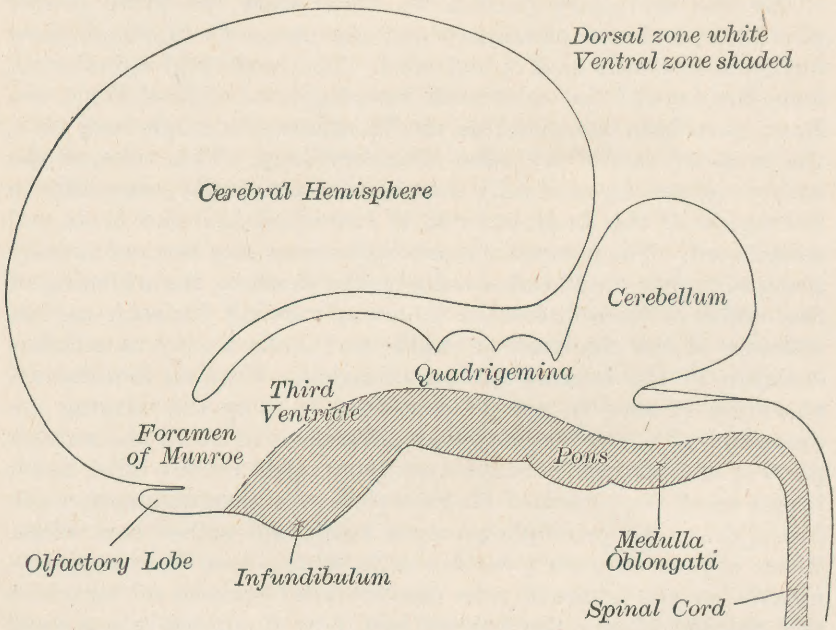
Let us now attempt to acquire fuller and more exact conceptions in regard to the four discoveries above enumerated. We may hope to do this without entering into technical details and with the use only of terms readily understood. At the same time we shall learn wherein the significance of the four discoveries lies.

THE FIRST DISCOVERY.—The division of the nervous system into a medullary portion and a ganglionic portion has to be explained. The division has long been a familiar fact to anatomists, but its true character and fundamental significance have been known a short time only, because it is owing to very recent embryological discoveries that the independent development of the ganglionic portion has been elucidated. The existence of the ganglia has long been known, but their development independently of the rest of the nervous system is a new conception. Their independence is, of course, not absolute but relative, for every part of the body develops in intimate relations with, and in dependence upon, the neighboring parts.

By the medullary portion we understand the brain proper plus the spinal cord or marrow and the nerve fibers, which grow out from the brain and spinal cord. The brain and spinal cord, since the days of the celebrated investigations of Karl Ernst von Baer, have been identified as modifications of a single long tube, the so-called medullary tube of embryology. This tube, as the embryo advances, gradually increases in complexity, especially in the region of the head, until it is converted into the brain and spinal cord. The complications which occur may be conveniently grouped under four heads—namely, the flexures, the widening of the cavity or its obliteration in a way varying for each region, changes in the thickness of walls, and lastly an extreme differentiation of the microscopic organization. Without detailed explanation it may be readily conceived that by the varying cooperation of these factors great differences arise in the sundry parts of the originally simple medullary tube. On the other hand, in the most fundamental characteristic, the production of nerve fibers, the same principle governs brain and spinal cord alike. There appear very early certain cells, which soon become recognizable as young nerve cells (neuroblasts) because of their size and pointed shape; the pointed end now elongates into a very delicate thread, the nerve fiber, which is at first very short but rapidly lengthens almost like a growing root; the growing fiber takes its course for a certain distance, varying according to circumstances, within the wall of the medullary tube, but ultimately passes outside the tube into the neighboring tissues together with other nerve fibers of similar origin. It must be added that some of the nerve fibers are of the Golgi type—that is to say, they end as well as begin within the central nervous system. The bundle of nerve fibers which pass out together constitute a nerve, or, to speak more correctly, a nerve root. So far as yet observed no exception occurs; therefore we may safely assert that every nerve cell of the brain or spinal cord produces one nerve fiber and only one, and this fiber grows out from the nervous system into the

tissues of the body. The fiber is single at its origin, but since we always find the peripheral fibers branching, we may add that the fiber is multiple at its termination. The nerve cells acquire also other secondary branches—the so-called protoplasmatic processes or dendrites—which grow out from the cells, but are not nerve fibers and are confined in their growth to the nervous tissue itself. The secondary branches present highly characteristic variations in the different regions of the brain, as described in the text-books.

By the ganglionic portion we now understand the nerve cells which lie in little groups outside of the medullary tube. These cells produce fibers, which grow in two directions—on the one side into the brain or spinal cord, on the other away from the



brain and cord into other tissues and organs. It has been observed that the ganglionic nerve cells elongate and become spindle-shaped; each pointed end of the cell grows out into a nerve fiber; as the nerve cell connects the two fibers, we may describe the actual condition accurately as resulting in a single nerve fiber, which has a nerve cell interpolated in its course. Each group of nerve cells forms a bundle of nerve fibers, which constitute the posterior (or so-called dorsal or sensory) root of the anatomists. If we follow a ganglionic fiber into the spinal cord or brain, we find that it forms two branches, as first recorded by Ramon y Cajal, a distinguished Spanish histologist; of these two branches, one runs upward, or in the brain forward, and the other runs downward, or in the brain backward; each fork gives off second-

ary branches (collaterals), that ramify still further, and are all situated within the central nervous system proper. If we study the termination of the ganglionic fiber at its other end—that is to say, in the tissues or organs—we find that there also there occur several ramifications. These fibers, like the medullary fibers, have each a single origin, but, unlike the medullary fibers, have *two* sets of multiple terminations. Although both the peripheral and central terminations have been carefully studied, they have never been found connected with other structures or cells, but only to be in contact with them.

The true history of the ganglia and their nerve fibers has been elucidated chiefly through the masterly researches of Wilhelm His, Professor of Anatomy at Leipsic, who is the recognized highest living authority on the development of man. This addition to our knowledge of the nervous system is perhaps the most important which has been made during the last generation. It teaches us that the nervous system comprises two sets of nerve cells and fibers, which differ not only in their situation, but also in their development and distribution. We are already in a position to say that the entire physiology of the brain must henceforth be based upon this discovery of the independence of the ganglionic system, because the same laws can not apply without change to structures so differently organized as are the two portions which we have briefly characterized, and there can be no doubt that the functions are as fundamentally divergent as is the organization. It is, however, still too soon for cerebral physiology to have remodeled itself, but that remodeling must follow, since physiology always bases itself on the anatomical facts.

Besides the two classes of nerve fibers, the medullary and ganglionic, we may have to add a third. In the organs of special sense (sight, hearing, smell, and taste) there are found the peculiar sensory cells, which all present two special features: First, they have characteristic modifications of cellular structure, by which they are adapted to receive sensory impressions; second, they are each united with a single nerve fiber. It has long been, and indeed still is, the prevalent theory that the nerve fiber arose from the brain, grew to the cell, and united with it. Merkel was, I think, the first to suggest that the sensory cells are also true nerve cells, the nerve fiber springing from them and growing to the brain. This view has been brought into fresh prominence by the discovery made by Michael von Lenhossék that Merkel's supposition is true in the case of the earthworm, which has cells scattered in its skin, each cell giving rise to a nerve fiber, which must arise from the sensory cell since it is connected with no other cell, although it enters the central nervous system and there ramifies.

THE SECOND DISCOVERY.—For the recognition of the three

sets of nerve roots also we are indebted to the researches of His, published in 1888. Previous to that time anatomists recognized two roots only—the posterior or dorsal roots, and the anterior or ventral roots. In the spinal cord it was easy to maintain Bell's law, that the posterior roots are sensory; the anterior, motor or efferent. The cephalic nerves, however, could not be brought into accord with this law, because of numerous difficulties, of which one may be mentioned as an example. The nerve called the facial was found physiologically to be both sensory and motor, and yet was shown embryologically to correspond to a posterior root. Through His we learned that the cephalic nerves corresponding to the posterior roots have in reality compound roots, being double. In fact, the nerves of the class referred to consist each of a bundle of ganglionic fibers which enter the brain and branch in its dorsal regions, and of a bundle of medullary fibers, which arise in the ventral portions of the brain and pass out from it immediately below the entrance of the ganglionic fibers. Evidently there are two roots, which, from their close juxtaposition, have been hitherto unrecognized; the ganglionic bundle is the *true dorsal root*, the medullary bundle the *lateral root*. If, now, we modify Bell's law by saying that all medullary fibers are efferent or motor, and all ganglionic fibers afferent or sensory, we can understand the double function of the facial nerves and of the other nerves resembling it—to wit, the trigeminal, glosso-pharyngeal, and vagus.

The recognition of the lateral root as distinct from, though joined with, the dorsal sensory root, removes many obscurities in the anatomy of the nervous system. We know that lateral roots are not confined to the nerves of the head, but they also occur in the upper cervical nerves, and I regard it as highly probable that with the progress of research they will be found sharing in the formation of other spinal nerves. Should this expectation be fulfilled, the long-established conception of the posterior roots as purely sensory will have to be modified, although it has reigned for three quarters of a century as one of the fundamental conceptions of physiology.

THE THIRD DISCOVERY.—The third discovery is that neither the nerve cells nor nerve fibers are directly continuous either with other nerve cells or with the cells or structures of other tissues and organs. Every nerve cell, together with its fiber, is an entity, and is not organically continuous with anything else. It is certainly premature to affirm this discovery positively, for we can say at present only that the consensus of the best opinion, of such men, for instance, as His and Kölliker, is in favor of the conception that every nerve cell plus its nerve fiber is an isolated element. Until recently the hypothesis was received with favor that

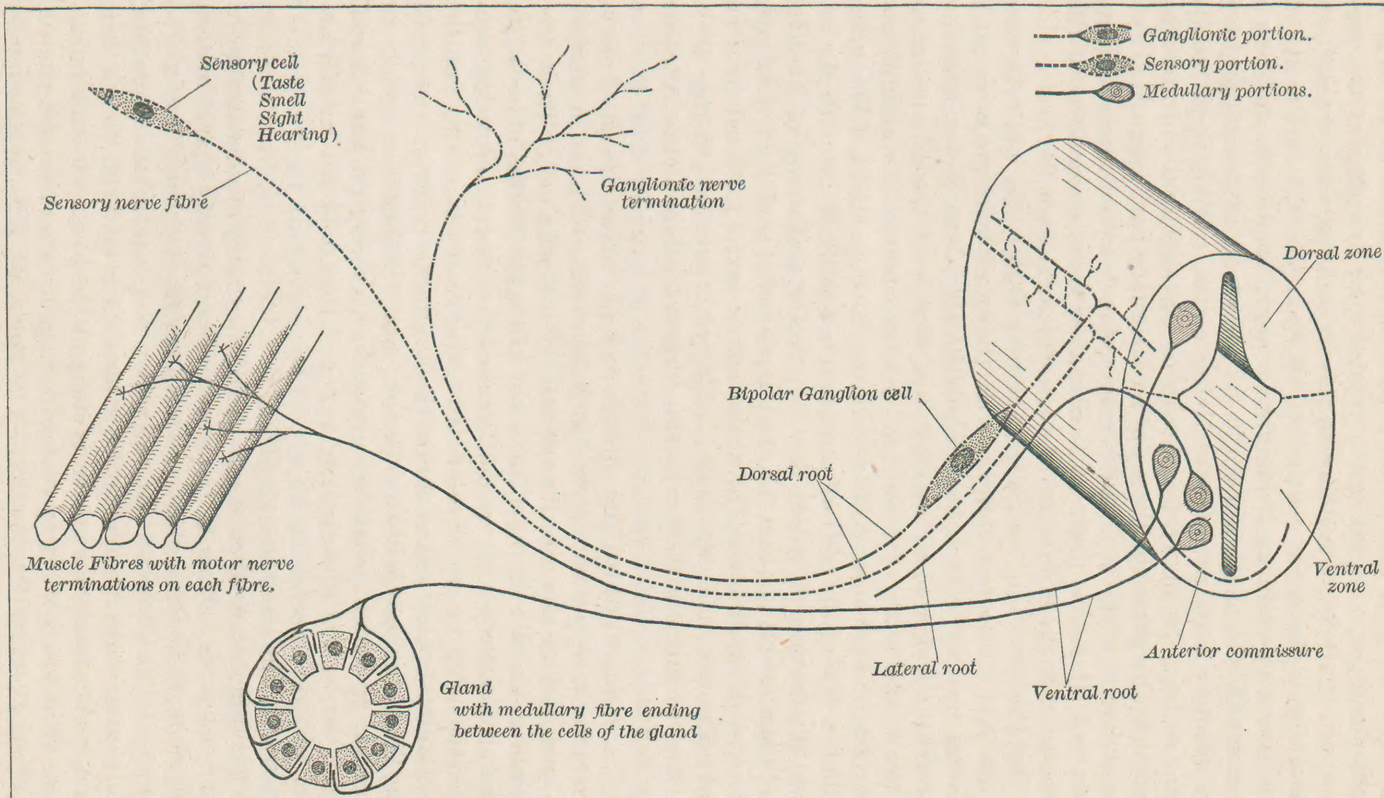


DIAGRAM TO SHOW THE ORIGIN AND TERMINATIONS OF NERVE FIBRES.

the cells of brain and spinal cord were connected by threads of protoplasm, or, to speak more precisely, by branches of the processes of the cells; according to this hypothesis, there would be a direct protoplasmatic continuity between the different parts of the nervous system, and therefore a nerve impulse brought by a sensory fiber to the brain could be conceived as traveling along an uninterrupted pathway of living matter until it produced its final action. In many text-books of physiology there are diagrams to illustrate the theory of a continuous pathway. It is evident that if there is no such connection between nerve cells as assumed, then we must radically alter our conceptions of the process of the transmission of nerve force through the brain.

In the question before us, Camillo Golgi and his followers must lead the way. Golgi, whom the world will probably rank among men of genius, has unquestionably done more than any other man living to enlarge our knowledge of the minute structure of the brain, for we owe to him, besides invaluable researches, the invention of an entirely novel method of study, by which a few of the cells of the brain are marked out with the utmost distinctness by a deep deposit of color, while most of the cells and tissues of the brain are left translucent and lightly tinged. The finest ramifications of these cells can be followed in such preparations under the microscope; yet they have never been proved to unite with the ramifications of other cells. Another method is that which consists in treatment by chloride of gold, as long employed in histology for tracing the finest thread of nervous substance, yet with this also it has hitherto been impossible to demonstrate any actual continuity of cell with cell. There are, however, certain authorities who still uphold the older view. Thus Adam Sedgwick, guided by certain general theoretical considerations as to the laws of cell connection, expects to find the continuity hypothesis re-established. Recently Prof. Dogiel, of the Siberian University at Tomsk, has published an article in Russian, in which he apparently seeks to verify the same hypothesis by actual observation, but unfortunately his results are not yet fully accessible to me. The settling of the problem is beset with the greatest difficulties.

The physiological consequences of the theory of non-continuity reach very far. Thus, if the sensory fibers simply branch within the brain, then there must occur a leap from those fibers to the cells which are to send out the reflex response to the sensation. So in other cases there must be a leap from one cell to another. Perhaps the leap or transfer is comparable to an electric induction. But it is obviously useless to ramble into sheer speculation.

THE FOURTH DISCOVERY.—The zones of His were vaguely recognized by Löwe, but to His belongs the honor of having first

clearly recognized them and established their morphological importance. There are four zones of His—two on each side; they run the entire length of the brain and spinal cord, except that in the partially aborted end of the latter the zones are imperfectly developed. Each zone is a thickening of the wall of the medullary tube. We distinguish the dorsal and ventral zones. The dorsal zone was termed by His the *Flügelplatte* (wing plate) and the ventral zone the *Grundplatte* (basilar plate), but the new names proposed appear to me preferable. At an early stage of development the two zones are very clearly marked off from one another; but after a more advanced stage is reached, although they preserve their characteristic differences, their delimitation is far less conspicuous. They persist throughout life, and can be identified in the adult. Thus, for example, in the cerebral region proper, or, as commonly termed, the region of the third ventricle, is a groove known as the sulcus of Munro, which runs from the opening which is termed the foramen of Munro, along the lateral wall of the ventricle, backward to the narrow continuation of the ventricle which has received the fanciful name of the aqueduct of Sylvius. This groove, the exact position of which I have thus indicated for the sake of possible anatomical readers, is the boundary between the dorsal and ventral zones. The superficial character of our previous knowledge of the brain is emphasized by the fact that the sulcus of Munro is usually not mentioned or figured in anatomical text-books, and yet we can say now that it is the most important landmark to be found in the part of the brain in which it occurs. It will suffice to give one other example: In the spinal cord the structure known by the name of the posterior fissure—a singular misnomer, since it is not a fissure—arises by the growing together of the two dorsal zones; a line drawn from the bottom of the so-called posterior fissure to the entrance of the posterior nerve roots would represent approximately the boundary between the dorsal and ventral zones. These two examples can, of course, be clear only to anatomists, but they demonstrate the permanency of the zonal divisions.

We have already learned that the fibers which arise from the nerve cells of the ganglia outside the nervous system proper enter the dorsal zone of His and there fork, the forks running longitudinally within the zone but in opposite directions. Gradually the number of fibers running in the zone increases until they form a fibrous tract of considerable size. The tract is originally situated next the outer surface of the nervous system; in the case of the spinal cord it remains permanently upon the outside, and therefore, as the nerve fibers ultimately become white in color, there is the so-called "white substance" covering the outer portion of the dorsal zone of the spinal cord, and it is this covering, which is

known anatomically as the posterior columns,* and which overlies all the medullary nerve cells that form part of the interior or "gray matter." In the brain also there enter several nerves, the ganglionic fibers which are distributed in precisely the same way as those just described—that is, they produce a superficial layer in the dorsal zone; they may be seen in this position during early stages in the part of the brain (medulla oblongata) adjoining the spinal cord. By secondary processes there follows a spreading of the nervous tissues over the outside of this white matter. We then have a white matter buried and isolated, but it remains, what it was primitively, the direct continuation of the superficial layer of the spinal cord. The bundle of nerve fibers is known as the solitary tract. Although the relations are complicated and not easily rendered clear, I hope enough has been said to demonstrate that the dorsal zone always remains what it is at first—the zone into which the ganglionic fibers enter and in which they chiefly ramify.

As every one knows, the two largest divisions or parts of the human brain are the cerebrum or hemispheres and the cerebellum. These, we have now learned, are both structures developed exclusively from the dorsal zones of His, and have therefore a very different morphological value from what has hitherto been assumed—not being modifications of the whole brain, but only local developments of the dorsal half of the brain. Just as primitively the medullary fibers which arise in the dorsal zone pass into the ventral zone, so in the specialized cerebral hemispheres and in the cerebellum there arise very numerous nerve fibers, but these still obey the primal law and take their courses into the portions of the brain representing the ventral zones, and thence the fibers are distributed to their various destinations. Until the relations of the zones to the nerve fibers, on the one hand, and to the hemispheres and cerebellum on the other, had been embryologically determined, it could not be known that the course of the cerebral and cerebellar fibers is in accordance with a fundamental law of nervous organization. We can foresee, though somewhat vaguely, that essential physiological deductions will follow the application of the law to the study of the functions of the brain.

The relations of the zones in the entire brain are indicated by the diagram on page 4, which scarcely calls for comment, since it sufficiently explains itself. I need only add that the position of the dividing line of the zones in the region of the corpora quadrigemina is somewhat uncertain. In the embryo this region

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* Including the postero-lateral columns, the columns of Burdach, and perhaps also the columns of Gol.

is known as the mid-brain, and shows the primary division very clearly; but as the further development has not been worked out properly yet, we can not decide positively as to the exact demarcation of the zones in the adult.*

The ventral zone of the brain may be defined, as we have already learned, as the territory of the medullary fibers, for it furnishes the pathway for those fibers to collect in bundles, which may either form nerve roots (ventral or lateral), or may cross, as so-called commissural fibers, from one side to the other in order to establish the nervous connection between the two halves of the brain or spinal cord. Most all the nerve fibers produced within the brain enter the ventral territory, for in this territory we observe not only the fibers which it obviously must include—namely, those which are produced by the nerve cells of the ventral zone—but also the nerve fibers produced by the nerve cells of the dorsal zone. So far as at present known, the nerve cells of the dorsal zone all produce nerve fibers, but these fibers always pass into the ventral division of the nervous system. These fibers of dorsal origin are the chief, perhaps the only ones, which are commissural—that is to say, which pass to the opposite side of the brain; others of these fibers take longitudinal courses within the ventral zone; while still others participate in the formation of the nearest ventral (or anterior) nerve roots. If, therefore, we assume that the sensory nerve impulses are carried into the dorsal zone and there transferred to the medullary nerve cells, we must conclude that from those cells the impulse may be sent along medullary fibers either into the opposite side, or up and down the ventral zone, or into a neighboring nerve root. The center of divergence is the dorsal zone, but the actual divergence of the fibers takes place in the ventral zone.

Although the ventral zone receives medullary fibers and itself produces nerve fibers, it sends, so far as yet observed, no fiber into the dorsal zone, but all the fibers which leave the ventral zone form nerve roots and leave the nervous system altogether. These roots, as we have already learned, are in two sets—the lateral and ventral.

SUMMARY.—The numerous facts which we have marshaled in hasty review so greatly widen our knowledge of the nervous system that it is important to render them as clear as possible. If what has been presented be critically considered, it will be found that what we have gained is an enormous accession of knowledge

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* I am led to suppose that the dorsal zones of the mid-brain unite, but that the ventral zones do not, and that therefore the aqueduct of Sylvius lies entirely between the ventral zones, the dorsal portion of the original cavity in that region of the brain being obliterated. It is very possible that this supposition is incorrect.

in regard to the nature, origin, distribution, and connections of nerve fibers. In order to make the typical variations of nerve fibers as evident as possible, I have constructed the accompanying diagram, which is, I think, correct for all which it attempts to give. We notice: *First,* that the central nervous system is a medullary *tube,* the walls of which form two dorsal zones and two ventral zones. *Second,* that every nerve fiber arises from a single cell only, and is nowhere united with any other cell. *Third,* that every nerve fiber has a branching termination. *Fourth,* there are three kinds of nerve fibers: (1) Medullary, which arise from the nerve cells of the central nervous system proper; of the medullary fibers three kinds are distinguished—namely, those which pass out to form the ventral root, those which pass out to form the lateral root, and those which pass as commissures to the opposite side of the tube; there are also medullary fibers which run lengthwise of the nervous system, but these are not represented in the diagram; second, ganglionic fibers, which run from the bipolar ganglionic nerve cells in two directions, and have two terminations, one branching within the medullary tube, the other branching to form peripheral sense organs; third, peripheral sensory fibers, which spring from the nerve-sense cells; that fibers of such origin exist is well known, but that they enter the central nervous system and there ramify, as here depicted, has as yet been actually demonstrated only in the earthworm. *Fifth,* that all the ganglionic and peripheral sensory fibers enter the dorsal zone only, while all the medullary fibers make their exit from the ventral zone only.

If we can reason from the structure, we must conclude that all the complicated functions of the brain depend upon four primary sets of functions—*namely,* 1, 2, and 3, the functions of the three classes of nerve cells, together with their connected fibers; and 4, the function of transferring nerve impulse from one fiber to another. Until physiologists and psychologists shall have learned to differentiate the four sets of functions, and have invented successful means for their separate investigation, cerebral physiology is, in my opinion, likely to remain, what it has so long been, a science of unsolved problems.